WATER SURFACE WAVES GENERATED BY THE MALE PISAURID SPIDER *DOLOMEDES TRITON* (WALCKENAER) DURING COURTSHIP BEHAVIOR

Horst Bleckmann[1] and Manfred Bender

Gruppe Sinnesphysiologie, Zoologisches Institut der Johann Wolfgang Goethe-Universität, Siesmayerstrasse 70, 6000 Frankfurt am Main Federal Republic of Germany

ABSTRACT

The semi-aquatic spider *Dolomedes triton* inhabits the littoral zone of ponds and lakes. During the mating season male *D. triton* perform displays consisting of leg-waving, single or successive jerks, and palpal drumming. The jerks cause bursts of concentric water surface waves which may provide information for the female. Jerk-generated waves are considerably regular in the time course, have a duration of 900 ± 145 ms, and do not contain frequencies above 55 Hz. In contrast, terrestrial insects trapped at the water surface generate wave stimuli which are long lasting (in most cases > 2 s), irregular in the time course, and usually include frequencies above 55 Hz (Lang 1980; Bleckmann 1985a). Thus wave signals produced by male *Dolomedes* during courtship behavior lack "prey" (insect) wave characteristics, which may ensure that female *Dolomedes* and other surface dwelling predators do not regard the courting males as insect prey.

INTRODUCTION

The fishing spider *Dolomedes triton* (Walckenaer) inhabits the littoral zone of lakes and ponds (Carico 1973; Bleckmann and Rovner 1984). Fishing spiders prey opportunistically on aquatic- and semiaquatic insects, as well as terrestrial insects that have fallen into the water (Carico 1973; Williams 1979; Bleckmann and Barth 1984). In addition these spiders catch vertebrates such as small fish, frogs, and tadpoles (Gudger 1922; Bleckmann and Lotz 1987). *D. triton* detects, recognizes, and localizes its prey with the aid of water surface waves (Bleckmann and Barth 1984; Bleckmann and Lotz 1987). Terrestrial insects trapped at the water surface generate wave stimuli which are long lasting (in most cases > 2 s), irregular in the time course, and usually include frequencies above 55 Hz (Lang 1980; Bleckmann 1985a). Consequently, artificial wave stimuli with these characteristics effectively elicit prey capture behavior in *Dolomedes* (Bleckmann and Barth 1984; Bleckmann 1985a).

Fishing spiders live in a complex vibratory environment. Not only prey objects, but abiotic sources such as leaf, seed, or twig fall also generate water surface waves. These types of wave stimuli are short-lasting (< 1 s, Bleckmann 1985a), have a regular time course (if compared with insect waves), and rarely contain

[1]Present address: Fakultät für Biologie, Universität Bielefeld, Postfach 8640, D-4800 Bielefeld 7, Federal Republic of Germany.

frequencies above 50 Hz (Lang 1980). The same holds for the waves generated by small fish, toads, and tadpoles when they contact the water surface (Bleckmann and Lotz 1987). *D. triton* responds to this type of wave stimulus in less than 2% of the cases with prey capture attempts (Bleckmann 1985a; Bleckmann and Lotz 1987). Wind-generated water surface oscillations constitute a third type of vibration with which fishing spiders have to deal. Wind-generated wave stimuli do not have frequencies above 10 Hz (Bleckmann and Rovner 1984). Like web spiders (Klärner and Barth 1982; Masters 1984) and spiders hunting on a solid substrate (Hergenröder and Barth 1984), *D. triton* rarely can be induced to attack a vibrator below a frequency of 10 Hz (Bleckmann and Barth 1984).

During the mating season male *Dolomedes* perform displays of leg-waving, palpal drumming, and jerks. The jerks, especially, cause easily visible bursts of concentric surface waves, which may provide information for the female (Roland and Rovner 1983). This raises the question whether and how the wave stimuli generated by the courting male differ from prey waves and water disturbances caused by abiotic sources. To solve this question we have recorded surface waves caused by male *D. triton*. Our experimental results show that jerk-generated wave stimuli resemble abiotically or vertebrate-generated wave stimuli in many aspects, i.e., they have a regular time course, a mean duration of less than 1 sec, and an upper frequency limit which rarely exceeds 55 Hz. This suggests that courtship signals are unlikely to be misinterpreted as insect prey stimuli by female *Dolomedes* or by other surface-dwelling predators (Bleckmann 1985b).

GENERAL METHODS

We used mature male and female *Dolomedes triton* for the experiments. All the spiders were collected in Athens, Ohio, USA, and housed individually in small jars (diameter 13-15 cm). The jars, which were filled a few cm deep with fresh water, contained a floating piece of styrofoam, serving as a resting site. The spiders were fed once a week with at least one fly (*Calliphora vicina*). We blinded all spiders by covering their eyes with correction fluid (Tipp-Ex = Liquid Paper®), because intact *Dolomedes* tend to respond to the slightest movement of the experimenter with fright reactions (Bleckmann and Barth 1984), thus being less suitable for experimentation. Spiders were given at least one day to acclimate to the blindess. For the experiments, we introduced a female spider to the experimental tank (50 x 60 cm, water depth 5.5 cm) and encouraged it to move around over the water surface. To minimize wave reflections, the experimental tank had a flat bank (slope 15-20°) covered with foam rubber. The entire experimental setup rested on air bags, which attenuated wave stimuli caused by vibrations of the building by at least 33 dB in the range 5-100 Hz (Bleckmann and Lotz 1987). After a waiting period of about 30 minutes, a male spider was introduced into the experimental tank on the side opposite the resting female. In most cases the male soon began with the first phase of courtship behavior.

The behavior of *D. triton* had been filmed previously with a a Cine-8 high-speed camera (Visual Instrumentation Corp., Model SP-1) at 100 frames per sec. We used a Lafayette Super 8 Analyzer (Model 926) with a frame counter to perform a frame-by-frame analysis.

A submerged emitter electrode, carefully placed close (5-10 cm) to the female spider, measured the wave stimuli. The method of wave measurement is based on
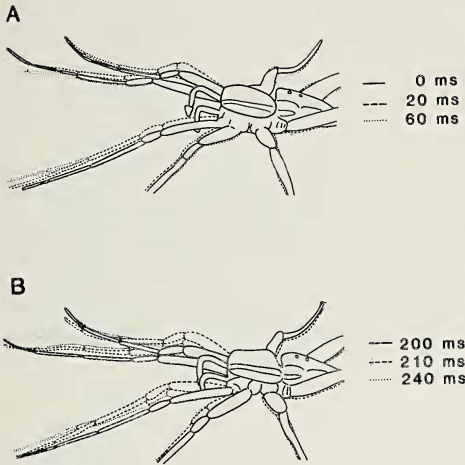
A

—   0 ms
---   20 ms
...... 60 ms

Fig. 1.—Leg movements of male *D. triton* during two successive jerks. The drawings are based on high-speed cinematography.

B

—— 200 ms
---- 210 ms
...... 240 ms

the principle that the electrical resistance between the emitter electrode inserted into the circuit of a Wheatstone bridge (Phillips PR 9307) and a receiver electrode depends on the depth of immersion of the latter. When the water surface is motionless, the Wheatstone bridge can be balanced. Any change in the water level at the receiver electrode disequilibrates the bridge and delivers in the range of 0-0.5 mm a voltage output which is linear to the wave amplitude. We stored the demodulated output of the Wheatstone bridge on an FM-tape (Howell CR 3000). For analysis the wave recordings were digitalized (Digital Equipment Corp., Minc 11; 512 data points, dwell time 3.1 or 3.9 ms), and stored on floppy disc for further processing. The frequency content of the wave stimuli was evaluated on the basis of the -60 dB bandwidth of the power spectra.

RESULTS

After introduction to the experimental tank which housed the female or after contacting the dragline of the female on land or water, male *D. triton* usually begin the first phase of signaling. This involves leg-waving and jerks (Roland and Rovner 1983). The former includes lifting legs I, usually in irregular alternation, with these legs typically being held extended straight or just slightly arched. Most often, the tarsus describes a vertically elliptical path. The leg-waving is presumably a long-distance visual signal (ibid.). At irregular intervals, while holding all the legs in contact with the substrate, the male performs one to three jerks. Each results from one or, more typically, two partial flexions and extensions at the femoro-patellar joint of legs I and, to a much lesser degree, legs II (Fig. 1). In the one case studied by single frame analysis, visible surface waves arose 20 ms after the initial jerk movement started. Then, 200 ms after the first jerk, which lasted for about 40 ms, the male displayed a second jerk which, within 30 ms, also generated a visible wave signal. In general, a noticeable effect of a jerk on water is a burst of concentric surface waves spreading outward from the male. In response to the male approach, the female may also generate water surface waves by rapidly vibrating her pedipalps. However, we did not attempt to record any female-generated wave stimuli.
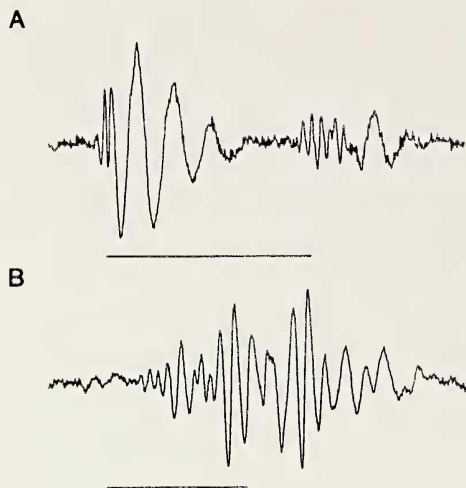
A

B

Fig. 2.—Two representative examples of jerk-generated wave stimuli produced by a single jerk (A) or by three successive jerks (B). The distance between the spider (reference point middle of the prosoma) and the wave measuring electrode is about 10 cm in A and 15 cm in B. Both stimuli were bandpass filtered from 10 to 1000 Hz. Time bar in A and B 500 ms.

Male-generated wave stimuli are sinusoidal and—if caused by a single jerk—click-like (Fig. 2A), i.e., these stimuli are short-lasting and have a regular downward frequency modulation which is probably caused by the dispersion relationship of capillary water surface waves (Sommerfeld 1970; Bleckmann and Schwartz 1982). If measured at a distance of 5-20 cm, wave signals generated by up to three successive jerks (Fig. 2B) have a mean duration of 900 ± 145 ms and an upper frequency limit of 55 Hz. The spectral amplitude maximum of these signals is found at around 7.3 ± 2.6 Hz (N=5, n=25) (Fig. 3).

DISCUSSION

The courtship signaling of spiders often exploits the predominant sensory modality in the prey detection system of the family or other taxon (Robinson 1982). Therefore it is not surprising that male *D. triton* use vibratory signals to court a female. In our experiments both the male and female spiders were allowed to move freely. The wave-measuring electrode was usually placed close to the female. However, the distance between the male and the wave-measuring electrode often exceeded 10 cm. Due to the strong damping of high-frequency water surface waves and the dispersion characteristics of the water-air interface (Sommerfeld 1970) our recordings may be biased—with respect to the waves a female experiences if close to the male—in that they have a too low upper frequency limit and a too long duration. However, the distance between male and female varies during courtship displays, i.e. depending upon the distance, the female will experience different wave stimuli. This makes it unlikely that the wave parameters of frequency content, duration, and amplitude have to be within a narrow range in order to transmit species-specific information. Female *Dolomedes* know the distance a wave signal has travelled (Bleckmann and Barth 1984), and there are strong indications that they weigh a wave stimulus according to that distance (Bleckmann 1987).

According to our results a wave stimulus produced by a single jerk is not very specific. Whenever the water surface is set into oscillation by a short-lasting (click-like) event, (i.e., by a falling leaf, seed, or twig) wave stimuli of short
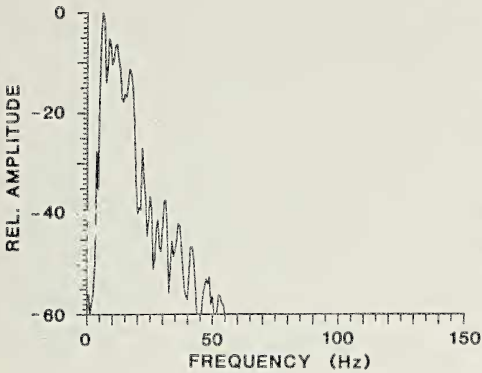
Fig. 3.—Representative example of the power spectrum of a jerk-generated wave stimulus produced by male *D. triton* during courtship display. Wave stimuli produced by one or two successive jerks were not distinguished.

duration, a regular time course, and a regular frequency downward modulation result (Bleckmann 1985a). The upper frequency limit of these stimuli rarely exceeds 50 Hz (Lang 1980; Bleckmann 1985a). As has been shown, click-like waves trigger prey capture behavior in *Dolomedes* in less than 2% of the cases even if the amplitude of these signals is far above threshold and the upper frequency limit reaches 78 Hz, i.e. includes frequencies unique to insect generated waves (Bleckmann 1985a). Thus even at close distance a courting male is unlikely to be misinterpreted as insect prey as long as it generates vibrations by a single jerk. The question remains, however, whether and how male-generated courtship stimuli can be recognized as such.

Male *Dolomedes* often perform two or even three jerks in quick succession. The upper frequency limit of 55 Hz and the mean duration of less than 1 sec still guarantees that these stimuli are insufficient to release prey capture behavior (Bleckmann 1985a). However, because a falling leaf or seed generates only one click at a time and place, it may well be that the quick repetition of two or even three jerks is one cue which enables the female to identify the male stimulus as such.

The best studied example of vibratory courtship behavior in spiders is that of the nocturnal Central American wandering spider *Cupiennius salei* (Keys.), which lives on banana plants, agaves, and bromeliads (Barth and Seyfarth 1979). Courting male *Cupiennius* produce a series of syllables, each of which consists of several impulses (Rovner and Barth 1981; Schüch and Barth 1985). The responsiveness of female *C. salei* to artificial courtship signals can be altered by changing the syllable duration, the intersyllable pause duration, or the syllable frequency content (W. Schüch, unpublished; Barth 1985). A single wave pulse generated by a courting male *Dolomedes* may be defined as a syllable. When approaching a female, a male *D. triton*, from time to time, generates a syllable. However, a regular timing of syllables was not discovered, at least not by simple visual observation.

Broadcast courtship displays are often replaced by low-range types of signals as soon as a mate has been attracted at close distance (Markl 1985). In addition to jerk-signals, male and female *Dolomedes* generate small, but visible, waves by palpal drumming. Although our recording device was not sensitive enough to detect these signals, it may well be that they contain additional species and sex-specific cues used by the female *Dolomedes* to identify a mate. Only careful further studies can show whether fishing spiders have a communication system

based on the exchange of vibratory signals equally sophisticated as that reported for some water striders (Wilcox 1972, 1979).

ACKNOWLEDGMENTS

REFERENCES

Barth, F. G. 1985. Neuroethology of the spider vibration sense. Pp. 203-229, *In* Neurobiology of Arachnids. (F. G. Barth, ed.). Springer Verlag, Berlin, Heidelberg, New York, Tokyo.

Barth, F. G. and E.-A. Seyfarth. 1979. *Cupiennius salei* Keys. (Araneae) in the highlands of central Guatemala. J. Arachnol., 7:255-263.

Bleckmann, H. and E. Schwartz. 1982. The functional significance of frequency modulation within a wave train for prey localization in the surface-feeding fish *Aplocheilus lineatus*. J. Comp. Physiol., 145:331-339.

Bleckmann, H. and J. Rovner. 1984. Sensory ecology of a semiaquatic spider (*Dolomedes triton*). I. Roles of vegetation and wind-generated waves in site selection. Behav. Ecol. Sociobiol., 14:297-302.

Bleckmann, H. and F. G. Barth. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behavior by water surface waves. Behav. Ecol. Sociobiol., 14:303-312.

Bleckmann, H. 1985a. Discrimination between prey and non-prey wave signals in the fishing spider *Dolomedes triton*. Pp. 215-222, *In* Acoustic and Vibrational Communication in Insects. (K. Kalmring and N. Elsner, eds.). Parey Verlag, Berlin.

Bleckmann, H. 1985b. Perception of water surface waves: How surface waves are used for prey identification, prey localization, and intraspecific communication. Pp. 147-166, *In* Progress in Sensory Physiology 5. (D. Ottoson, ed.). Springer Verlag, Berlin, Heidelberg, New York, Tokyo.

Bleckmann, H. and T. Lotz. 1987. The vertebrate catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). Anim. Behav., 35:641-651.

Bleckmann, H. 1987. Prey identification and prey localization in surface feeding fish and fishing spiders. Pp. 619-641, *In* Sensory Biology of Aquatic Animals. (J. Atema, R. Fay, A. Popper and W. Tavolga, eds.). Springer Verlag, Berlin, Heidelberg, New York, Tokyo.

Carico, J. E. 1973. The Nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). Bull. Mus. Comp. Zool., 144:435-488.

Gudger, W. E. 1922. Spiders as fishermen. J. Amer. Museum Nat. Hist., 22:565-568.

Hergenröder, R. and F. G. Barth. 1984. The release of attack and escape behavior by vibratory stimuli in a wandering spider (*Cupiennius salei* Keys.). J. Comp. Physiol., 152:347-358.

Klärner, D. and F. G. Barth. 1982. Vibratory signals and prey capture in orb-weaving spiders. J. Comp. Physiol., 148:445-455.

Lang, H. H. 1980. Surface wave discrimination between prey and nonprey by the backswimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). Behav. Ecol. Sociobiol., 6:233-246.

Liesenfeld, F. J. 1956. Untersuchungen am Netz über den Erschütterungssinn von *Zygiella x-notata* (Cl.) (Araneidae). Z. Vergl. Physiol., 38:563-592.

Markl, H. 1985. Manipulation, modulation, information, cognition: some of the riddles of communication. Pp. 163-194, *In* Fortschritte der Zoologie 31. (B. Hölldobler and M. Lindauer, eds.). Gustav Fischer Verlag, Stuttgart.

Masters, W. M. 1984. Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). II. Prey and wind signals and the spiders' response threshold. Behav. Ecol. Sociobiol., 15:217-223.

Robinson, M. H. 1982. Courtship and mating behavior in spiders. Ann. Rev. Entomol., 27:1-20.

Roland, C. and J. Rovner. 1983. Chemical and vibratory communication in the aquatic pisaurid spider *Dolomedes triton*. J. Arachnol., 11:77-85.

Rovner, J. and F. G. Barth. 1981. Vibratory communication through living plants by a tropical wandering spider. Science, 214:464-466.

Schüch, W. and F. G. Barth. 1985. Temporal patterns in the vibratory courtship signals of the wandering spider *Cupiennius salei* Keys. Behav. Ecol. Sociobiol., 16:263-271.

Sommerfeld, A. 1970. Vorlesungen über theoretische Physik, Bd. 2, Mechanik der deformierbaren Medien. Akademische Verlagsgesellschaft, Leipzig.

Wilcox, R. S. 1972. Communication by surface waves. Mating behavior of a water strider (Gerridae). J. Comp. Physiol., 80:255-266.

Wilcox, R. S. 1979. Sex discrimination in *Gerris remigis*: role of a surface wave signal. Science, 206:1325-1327.

Williams, D. S. 1979. The feeding behavior of New Zealand *Dolomedes* species (Araneae: Pisauridae). New Zealand J. Zool., 6:95-105.